

Two new species of flightless rails (Aves: Rallidae) from the Middle Pleistocene “crane fauna” of Bermuda

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Abstract.—Two new species of flightless rails are described from a Pleistocene fauna in Bermuda that also includes an extinct crane (*Grus latipes*) and an extinct duck (*Anas pachyscelus*). The medium-sized *Rallus ibycus*, new species, was possibly derived from North American populations of Virginia Rail (*R. limicola*), but had a longer bill, much more robust legs, and reduced wings and pectoral girdle. The very small *Porzana piercei*, new species, except for the reduced wing and pectoral girdle, is very similar to the extant Yellow-breasted Crake (*P. flaviventer*), which now occurs only in the Neotropics, including the Greater Antilles. The fauna that included these rails developed during a long, stable glacial period of lowered sea-levels in the Middle Pleistocene, during which the entire Bermuda platform was emergent. This was followed by an abrupt and extreme interglacial about 400,000 years ago when sea-levels rose to 21 m above present levels, obliterating most of Bermuda and much of its endemic fauna, including the rails.

The island of Bermuda, situated in the western North Atlantic 1050 km east of Cape Hatteras, North Carolina, is composed almost entirely of calcareous aeolianite on the southeastern rim of a submerged, truncated summit of an extinct volcano. The aeolianite has been modified by solution to form numerous caves and fissures that are accessible to collectors either through natural openings or through limestone quarrying operations. These caves frequently contain accumulated fossils of vertebrates and invertebrates, mainly birds and terrestrial gastropods. Although much of interest to avian paleontology has been collected from Bermuda, relatively little has been published, partly for lack of a better understanding of the complexities of the island's stratigraphy and chronology, which has been greatly improved in recent years.

The first contribution to knowledge of Pleistocene birds in Bermuda was that of

Wetmore (1960) who described a new genus and species of endemic crane, *Baeopteryx latipes*, and an extinct endemic duck, *Anas pachyscelus*, from the Wilkinson Quarry, Hamilton Parish. The genus *Baeopteryx* was later synonymized with typical cranes of the genus *Grus* (Fischer & Stephan 1971).

Wetmore (1960:10) mentioned that “the collection contains various bones from four species of rails, one very small, two of intermediate size, and one nearly as large as the modern clapper rail [*Rallus longirostris*]. These are not clearly marked in the present collection so that no attempt is made to describe them here in detail, particularly since complete material for one of them is now in other hands for study.” Actually, among the rail material that Wetmore examined, there are remains of only two species of rails, one medium-sized and the other very small (uncataloged specimens in

USNM). Wetmore's information on Bermuda rails apparently came in part from Pierce Brodkorb, University of Florida, who had been in Bermuda collecting fossil rails with Wingate only weeks before Wetmore's publication appeared. Later, Olson (1977:353–354) briefly mentioned the still undescribed fossil rails from Bermuda. Brodkorb's collections containing the Bermuda rails passed to the Florida Museum of Natural History after Brodkorb's death in 1992, and we have now belatedly begun the process of describing them.

Some information on the relationships and adaptations of the largest species of rail to which Wetmore alluded was provided by Olson (1997). This species was not contemporaneous with the "crane fauna" and does not appear to have co-existed with any other endemic rail on Bermuda. In February 1999, we discovered a new deposit in which this species was the predominant bird. Preliminary results from amino acid racemization ratios from associated snail shells indicate that it originated during a much younger glacial period. We have postponed description of this species until the new material can be fully prepared and analyzed. Here we describe the two species that are definitely part of the "crane fauna" that we believe dates back at least to the Middle Pleistocene.

Materials and Methods

The specimens obtained by Wingate and Brodkorb in 1960 were collected in association with bones of the extinct crane *Grus latipes*, from a vertical fracture on the eastern face of the Bermuda Government quarry in Hamilton Parish that was filled with soil and snail shells of the genus *Poecilonites* and was named the "Crane Crevice." The fossil birds, formerly part of the Pierce Brodkorb collection, are now cataloged in the Florida Museum of Natural History, University of Florida, Gainesville, and all take the prefix UF PB, which we have omitted except in the citations of the

holotypes and the figure legends. There are many more specimens available than are listed among the type material. As paratypes we have listed those specimens that were used in the descriptions, are illustrated, or were used for any of the cited measurements. Measurements of long bones of the limbs usually do not include broken or juvenile specimens, which accordingly are not among the paratypes listed. Measurements were taken with digital calipers to 0.01 mm and rounded to the nearest 0.1 mm.

Comparative material examined:—Skeletons (complete unless otherwise indicated) of the following species in the collections of the National Museum of Natural History, Smithsonian Institution (USNM), unless otherwise noted. *Amaurolimnas concolor* 613963; *Coturnicops noveboracensis* 556931; *Laterallus albigularis* 611563; *L. jamaicensis* 492195, 502495; *Pardirallus maculatus* 561272–76; *Poliolimnas cinereus* 560913; *Porzana flaviventer* 501640, 561276–78, and trunk skeletons 430043, 430931, 430979, 431339–41; *Porzana porzana* 552914; *P. albicollis* 562750; *P. atra* 562788; *P. carolina* 501052, 501671; *P. pusilla* 291704–05; *Rallus aquaticus* 431545, 553039, 553041, UF 34461; *R. limicola* 489973, 525915, 525917, UF 19598, UF 19769, UF 24324, UF 24322; *R. elegans* 499437, 525886, 610780; *R. longirostris* 525876, 525873, 525879; *R. longirostris* X *R. elegans* 525887.

Systematics

Family Rallidae

Genus *Rallus* Linnaeus

The very long, slender bill of the following species clearly places it in the genus *Rallus* in its strict sense (Olson 1973a). No flightless species of the restricted genus *Rallus* have been described previously. Such characters as are preserved in the fossils that are not obscured by flightless adaptations show no evidence of relationship to the species of *Pardirallus* (including *Or-*

tygonax), which also have long bills but are osteologically quite distinct and not especially closely related to *Rallus* (Olson 1973a).

Rallus ibycus, new species

Figs. 1–5

Holotype.—Premaxillary symphysis with anterior portion of internarial bar (pila supranasalis) UF PB5403. Collected in May 1960 by David B. Wingate.

Type locality.—Bermuda, Hamilton Parish, Government Quarry, Crane Crevice.

Chronology.—Middle Pleistocene, presumably within Oxygen Isotope Stages 13 to 20, approximately 800 to 450 kya (see discussion).

Measurements (mm) of holotype.—Length of premaxillary symphysis, 15.5.

Paratypes.—Premaxillary symphyses 5511, 5521. Pila supranasalis 5526. Crania 5401, 5512, 5518. Sterna 5402, 5430. Coracoids 5404, 5415, 5416, 5441, 5456. Humeri 5405, 5417, 5422, 5425–5426, 5428, 5457, 6063–6072, 6073, 6077, 6079. Ulnae 5406, 5423, 5440, 5458. Carpometacarpi 5407, 5419, 5424, 5439, 5459. Pelvis 5429. Femora 5409, 5432–5438, 5451, 5460, 5 uncataloged specimens. Tibiotarsi 5410, 5448–5449, 5452–5455, 5461, 5491–5492, 5498–5502, 5503, 5541–5542, 5551–5560. Tarsometatarsi 5442, 5444–5447, 5462, 5543–5546, 6001–6002, 6028–6031, 6055–6057.

Measurements (mm) of paratypes.—Rostrum: length from nasofrontal hinge estimated from 5526 and 5403 to be between 46.5 and 48.0; length of premaxillary symphysis 14.1, 15.5, 16.7. Cranium: length from naso-frontal hinge 28.0; width at post-orbital processes 15.5, 15.7; width of inter-orbital bridge 3.3, 3.6, 3.7. Coracoid: length 15.4, 17.4, 18.2, 18.4, 19.5. Sternum: length along midline (from anterior sternal notch, not manubrium) 21.2, 21.3; width across coracoidal sulci 10.7, 12.1; depth of carina 3.7, 4.4. Carpometacarpus: length 14.0, 16.1, 16.3, 16.5, 16.9; proximal depth 3.6,

4.1, 4.2, 4.3, 4.3. Ulna: length 22.8, 24.5, 25.8, 26.9. Pelvis: sacrum length 27.3, 30.0; width across antitrochanters 15.4. See also Table 1.

Etymology.—Greek, m. *ibykos*, literally of a crane, but here a noun in apposition referring to Ibycus (fl. 528 B.C.), a lyric poet whose murder was revealed by cranes (see Anthon 1869). The name is applied to the new species from its association with the much larger fossils of cranes, the discovery of which also revealed the extinction of the rail.

Diagnosis.—Similar in overall size to *Rallus limicola* but bill longer and more slender, with a longer and more decurved premaxillary symphysis. Flightless, with the sternum and pectoral elements reduced. Hindlimb elements much more robust.

Description.—In addition to the longer, more decurved bill, this species also seems to have the orbits reduced so the frontal area in lateral view has the appearance of sloping more steeply.

Compared with *Rallus limicola*, the sternum is shorter, wider, lacks a manubrial spine, and has a deep notch between the coracoidal sulci. The carina is very low and thick anteriorly, extending laterally as a rim, which, with the anterior ridge leading from the keel, creates a deep depression on the sides of the carina.

The shaft of the coracoid is narrowed, forming a sharp ridge from the head to mid-shaft. The procoracoid process is smaller, more delicate and pointed. The sternocoracoidal process is much more pronounced and pointed due to the deep circular incision in the external margin.

The humerus has the head lower and smaller, the capital groove deeper, the distal end narrower, with the tricipital grooves deeper. The ulna is shorter and stouter and slightly less curved. The carpometacarpus is very reduced, short, and stout.

The pelvis in dorsal view is decidedly wider, both anteriorly and posteriorly, although the ischial area in lateral view is not as deep as in *R. limicola*.

Table 1.—Measurements (mm) of selected skeletal elements of two new species of flightless rails from the Middle Pleistocene of Bermuda.

	<i>n</i>	Range	Mean	<i>SD</i>
<i>Rallus ibycus</i> , n. sp.				
Humerus				
Length	18	28.5–36.3	32.3	2.2
Proximal width	18	6.0–7.2	6.6	0.4
Shaft width	18	1.7–2.2	1.9	0.1
Distal width	18	4.0–4.8	4.4	0.2
Femur				
Length	16	34.9–41.5	37.9	2.6
Proximal width	15	5.7–6.9	6.4	0.3
Distal width	15	5.7–7.1	6.3	0.5
Tibiotarsus				
Length from proximal articular surface	28	45.7–55.5	50.5	3.4
Distal width	27	4.7–5.8	5.2	0.3
Tarsometatarsus				
Length	19	27.1–34.3	30.2	2.4
Proximal width	18	5.1–5.9	5.4	0.3
Distal width	18	5.1–6.1	5.6	0.3
<i>Porzana piercei</i> , n. sp.				
Humerus				
Length	54	19.7–23.2	21.4	0.7
Tibiotarsus				
Length from proximal articular surface	8	33.6–38.1	35.5	1.6
Distal width	7	3.1–3.4	3.3	0.1
Tarsometatarsus				
Length	25	19.9–23.9	22.3	0.9
Proximal width	25	3.1–3.6	3.4	0.1
Distal width	24	3.4–3.8	3.6	0.1

All of the elements of the hindlimb are extremely robust compared with *R. limicola*, with heavier shafts and more expanded articulations. The head of the femur is proportionately larger. The tibiotarsus and tarsometatarsus are proportionately shorter. The cnemial crests of the tibiotarsus are better developed, the fibular crest is longer, and the distal tendinal opening is larger. The tarsometatarsus has the trochleae more splayed, with the inner trochlea less elevated and retracted than in *R. limicola*.

Remarks.—The most likely progenitor of *R. ibycus* would be the Virginia Rail, *Rallus limicola*, a common migratory species in eastern North America that has been found as a “frequent but scarce vagrant” in Ber-

muda (Amos 1991:121). Rails described as being similar to *R. limicola* are known from the Pliocene and Pleistocene of North America (Olson 1977). The Eurasian Water Rail, *Rallus aquaticus*, is a less likely ancestor on geographic grounds, and also because of its larger size.

Genus *Porzana* Vieillot

The following new species of flightless rail from Bermuda is characterized by very small size and a short “crake-like” bill that invites comparison with the New World species of *Porzana*, *Laterallus*, and *Coturnicops*. Of particular concern is the Neotropical Yellow-breasted Crake, usually

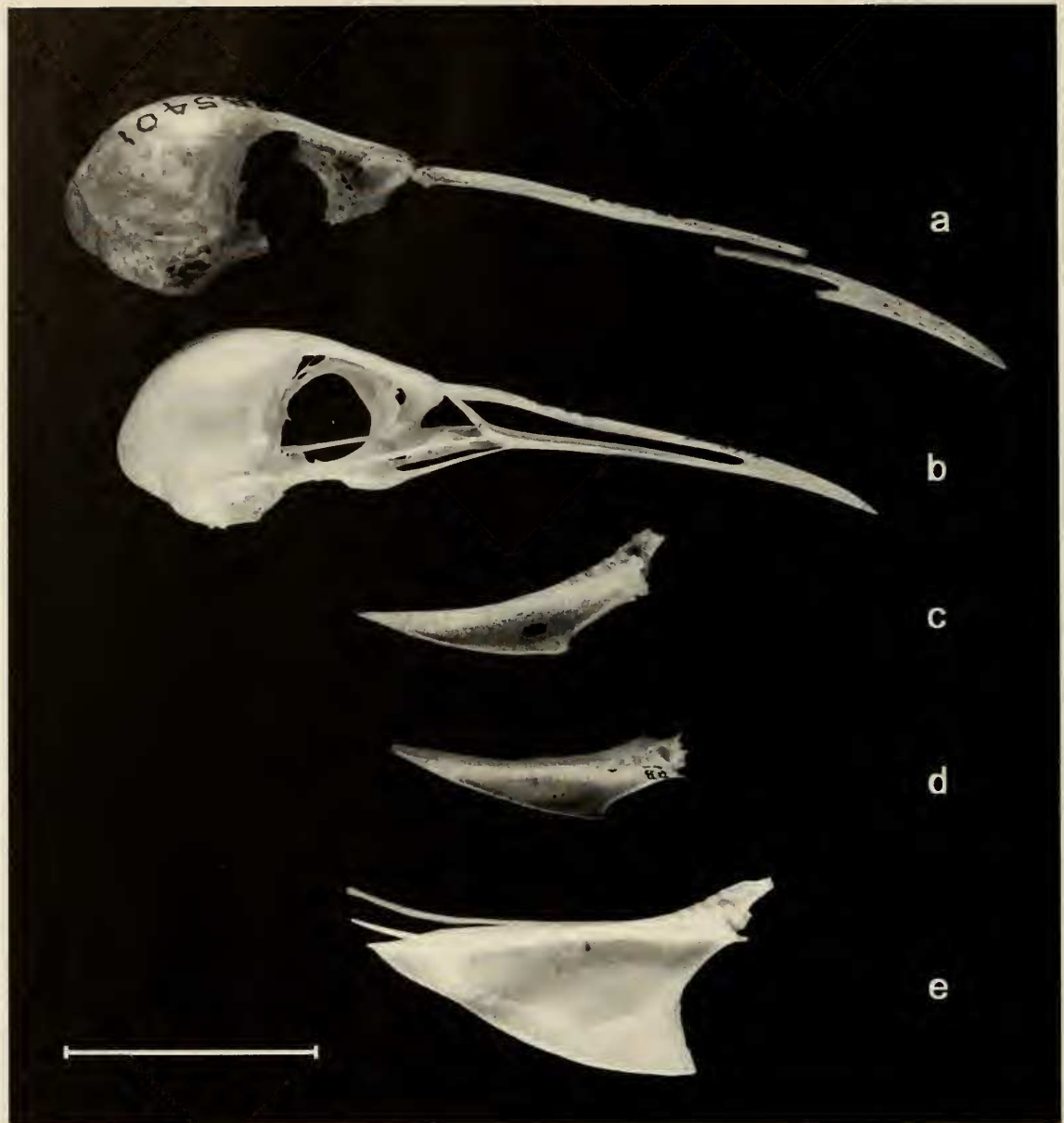


Fig. 1. Comparison of skulls (a–b) and sterna (c–e) of *Rallus* in lateral view. a, *Rallus ibycus*, new species (premaxillary symphysis, holotype UF PB5403; pila supranasalis UF PB5526; cranium UF PB 5401); b, e, *R. limicola* female USNM 525915; c, d, *R. ibycus* UF PB5430, UF PB5402. Scale bar = 2 cm.

known as *Porzana flaviventer*, for which Ridgway (1920) once erected the monotypic genus *Hapalocrex* (type *Rallus flaviventer* Boddaert). This species has little resemblance to the various species of *Porzana* with which it has been placed in most current literature. Using mostly external characters, Olson (1970) suggested that it be placed in the genus *Poliolimnas* with the Australo-Malayan species *P. cinereus*. Although a few authors have accepted Olson's conclusion (e.g., Short 1975), it has otherwise either been widely ignored or even sharply attacked (Mees 1982).

In an extensive morphological analysis of the Gruiformes emphasizing the Rallidae, Livezey (1998) found the relationships among the "crakes" and supposed allies to be difficult to resolve and even more difficult to reconcile with traditional taxonomy. The preliminary results of an extensive sampling of mitochondrial DNA sequences of the Rallidae indicate that the genus *Porzana* as now generally construed (e.g., del Hoyo et al. 1996), is an unnatural assemblage (Beth Slikas, National Zoological Park, pers. comm.). Until the taxonomic difficulties among the crakes can be better

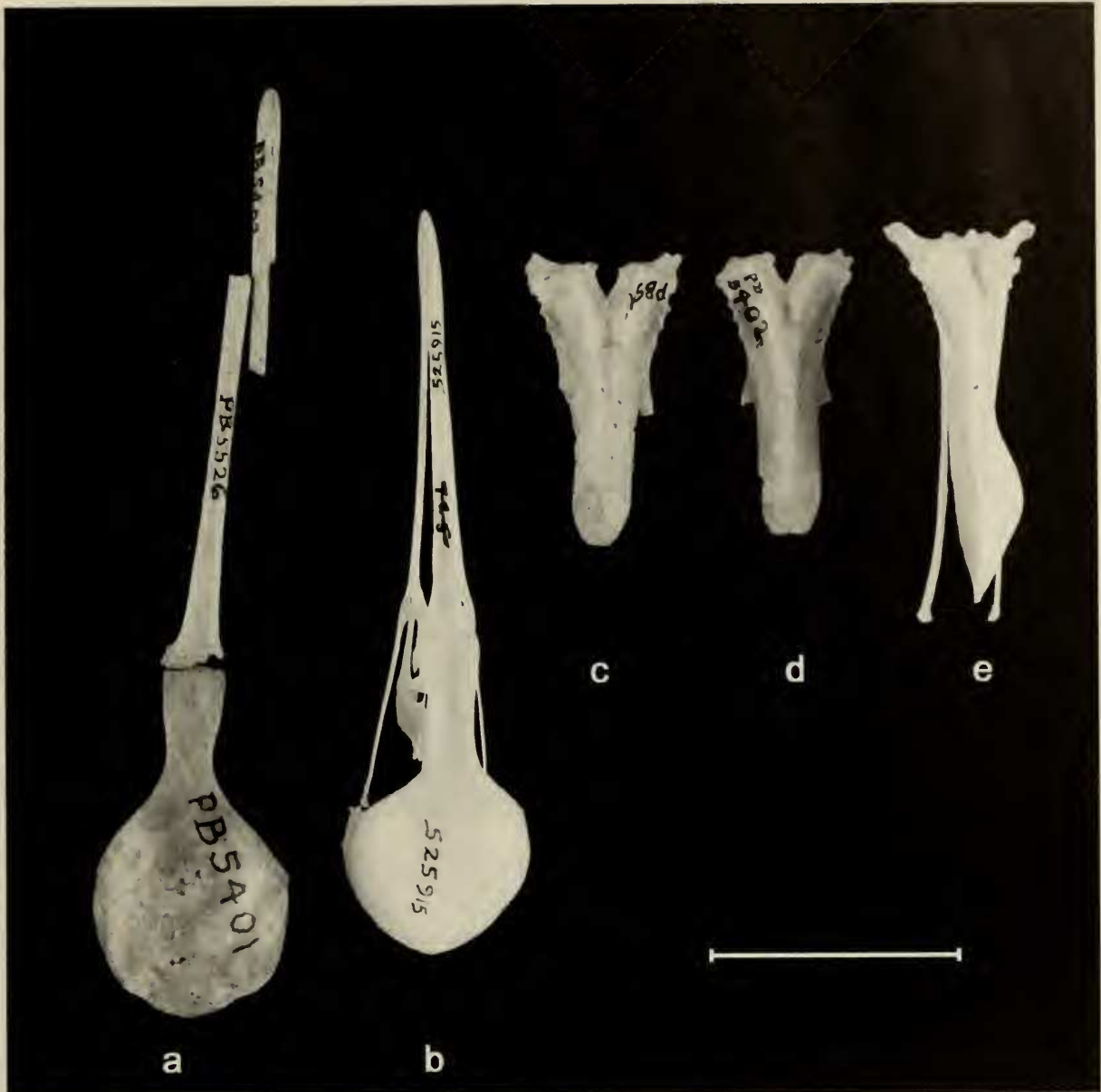


Fig. 2. Comparison of skulls (a–b) in dorsal view and sterna (c–e) in ventral view of *Rallus*. a, *Rallus ibycus*, new species (premaxillary symphysis, holotype UF PB5403; pila supranasalis UF PB5526; cranium UF PB 5401); b, e, *R. limicola* female USNM 525915; c, d, *R. ibycus* UF PB5430, UF PB5402. Scale bar = 2 cm.

resolved, we have chosen to continue with general usage in including *flaviventer* in the genus *Porzana*.

The fossil species from Bermuda compares as follows with other crakes from which it might have been derived. In *Laterallus* the nostril is shorter and higher, the premaxillary symphysis is shorter, and the interorbital bridge is wider. In species of *Porzana* except *P. flaviventer*, the nostril is longer and the premaxillary symphysis is shorter (except in *P. pusilla*, which has a long symphysis). In *Coturnicops* the bill is extremely short and deep, quite unlike the

fossil species. In the relatively short nostril, long premaxillary symphysis, and narrow interorbital bridge, the small Bermuda rail agrees perfectly with *Porzana flaviventer*.

A striking feature is the proportions of the hindlimb. When the hindlimb elements of *Porzana flaviventer* are compared with those of *Laterallus jamaicensis* it is seen that whereas the tibiotarsi are of nearly equal length, the femur in *P. flaviventer* is much shorter and all the elements are stouter. In *Coturnicops noveboracensis* the tibiotarsus is shorter yet the femur is longer than in *P. flaviventer*. Compared with other



Fig. 3. Comparison of pectoral and wing elements of *Rallus ibycus*, new species (a–e) with *R. limicola* (f–i, female USNM 525915). a, f, right coracoids in ventral view (a, UF PB5415); b, c, g, left humeri in palmar view (b, UF PB5422; c, UF PB6072); d, h, left ulnae in internal view (d, UF PB5458); e, i, left carpometacarpi in internal view (e, UF PB5407). Scale bar = 2 cm.

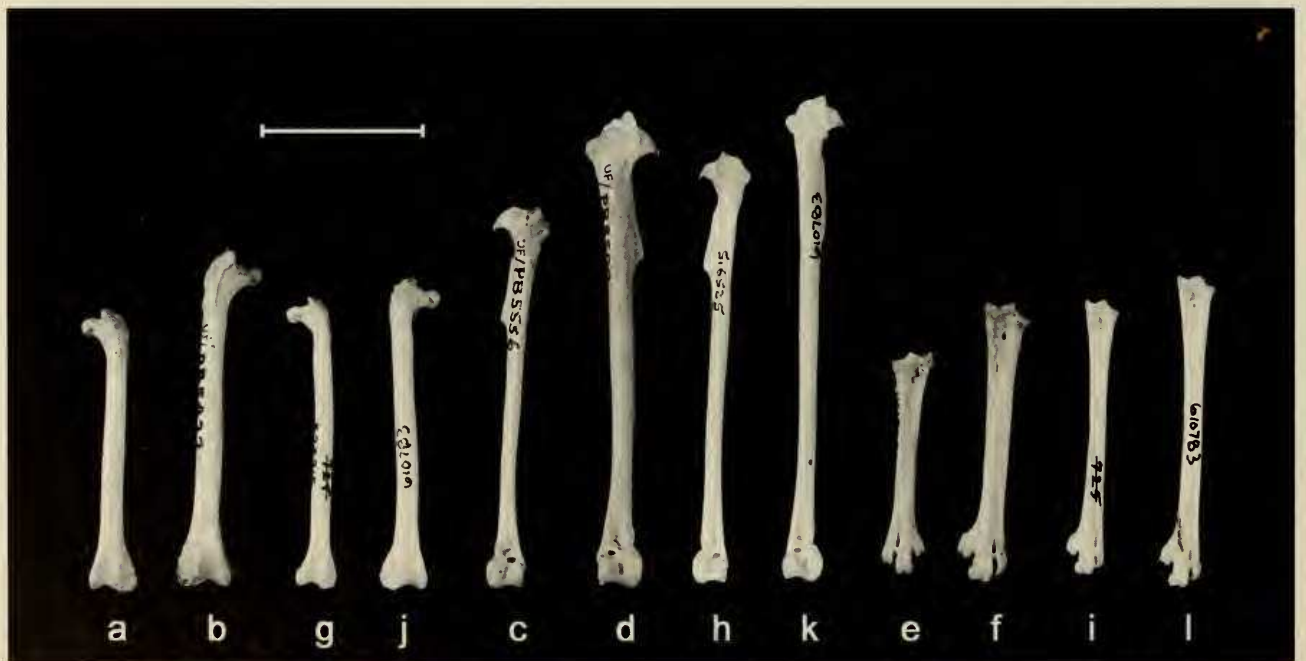


Fig. 4. Comparison of hindlimb elements in anterior view of *Rallus ibycus*, new species (a–f) with *R. limicola* (g–i, USNM 525915 female; j–l, USNM 610783 male). a, left femur UF PB5438; b, right femur UF PB5432; c, right tibiotarsus UF PB5556; d, left tibiotarsus UF PB5500; e, right tarsometatarsus UF PB5462; f, left tarsometatarsus UF PB5544. Scale bar = 2 cm.

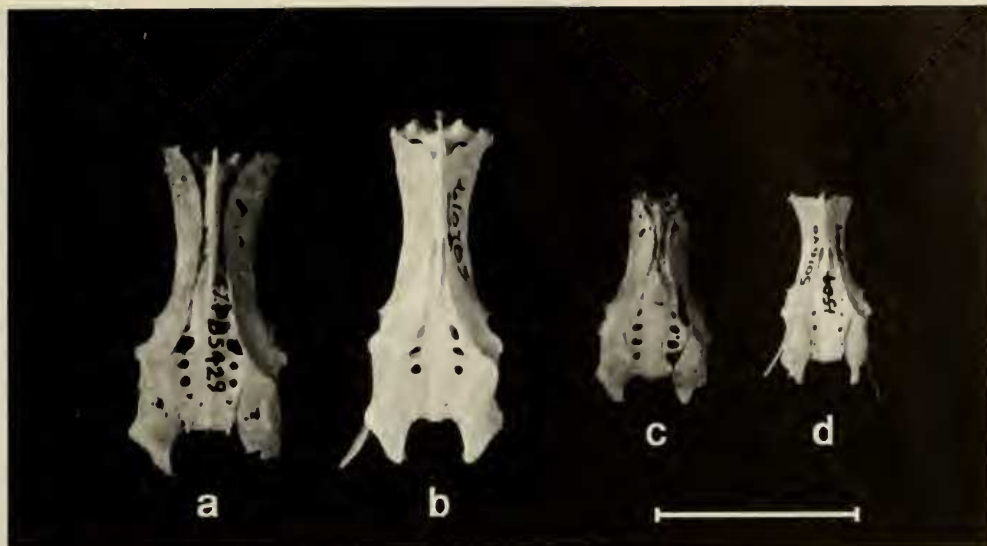


Fig. 5. Pelves of rails in dorsal view. a, *Rallus ibycus*, new species (UF PB5429); b, *R. limicola* (USNM 610783 male); c, *Porzana piercei* new species (UF PB5490); d, *P. flaviventer* (USNM 501640). Scale bar = 2 cm.

species of *Porzana*, the hindlimb elements of *P. flaviventer* are more likewise more robust, with the femur being proportionately shorter. As with the cranial elements, the hindlimb in the small Bermuda rail is most similar to that of *P. flaviventer*. The labels that Pierce Brodkorb left with the specimens indicate that he, too, had concluded that the small Bermuda rail was derived from *P. flaviventer*. The diagnosis of the new species is therefore based on its differences from that species.

Porzana piercei, new species

Figs. 5–9

Holotype.—Complete rostrum UF PB5413. Collected in March 1960 by Pierce Brodkorb and David B. Wingate.

Type locality.—Bermuda, Hamilton Parish, Government Quarry, Crane Crevice.

Chronology.—Middle Pleistocene, presumably within Oxygen Isotope Stages 13 to 20, approximately 800 to 450 kya (see discussion).

Measurements (mm) of holotype.—Length from nasofrontal hinge to tip, 16.8; length of premaxillary symphysis, 5.8.

Paratypes.—Rostra 5421, 5536–5540. Crania 5412, 5527–5528, 5533. Mandible 5481. Sternum 5414. Scapula 5482. Coracoids 5464, 5474, 5483. Humeri 5465,

5484, 5618, 5620, 5620 bis, 5621–5624, 5624 bis, 5625–5629, 5631–5633, 5635–5640, 5640 bis?, 5641–5643, 5645–5648, 5650–5651, 5653, 5654–5671, 5686, 6195. Ulnae 5466, 5485. Carpometacarpi 5476, 5487. Pelvis 5490. Femora 5468, 5478, 5488, 1 uncataloged. Tibiotarsi 5469–5471, 5510, 5547–5550. Tarsometatarsi (all rights except 5590 & 1 uncataloged with it) 3489, 5575–5585, 5587–5590 + 1 uncataloged, 5594, 5606–5607, 5617, 6060.

Measurements (mm) of paratypes.—Scapula: length 17.4. Coracoid: length 10.5, 10.7, 11.7. Ulna: length 16.6, 17.5. Carpometacarpus: length 11.0, 11.2. Pelvis: sacrum length 18.2, 19.0; width across antitrochanters 11.1, 11.6. Femur: length 25.0, 25.2, 26.2, 26.2; proximal width 3.8, 4.1, 4.2, 4.2; distal width 3.7, 3.9, 3.9, 4.1. See also Table 1.

Etymology.—Dedicated to the late Pierce Brodkorb who was instrumental in collecting rail material on Bermuda and who first recognized the affinities of this species.

Diagnosis.—Very similar to *P. flaviventer* but differing in having the skull and bill somewhat larger and in being flightless, with the sternum and pectoral apparatus reduced.

Description.—Compared with *P. flaviventer* the cranium is wider, the foramen

magnum larger, and the rostrum is wider with a shorter, wider premaxillary symphysis. The single specimen of mandible, a symphysis with the left dentary, is abraded at the tip but the symphysis is wider and deeper and the bone appears larger than in *P. flaviventer*.

The single available sternum lacks the lateral processes but clearly indicates a flightless species, as the body of the bone is much shorter, but slightly wider, with a much reduced carina that is lower and more posteriorly situated than in *P. flaviventer*. The sternocoracoidal processes are narrower and angled less dorsally in anterior view. The intercoracoidal notch is wider and the manubrial spine lacking.

The coracoids are reduced with more slender shafts and more delicate heads. The only available scapula has the articular end and anterior portion of the shaft wider, the acromion less pointed, and the glenoid facet larger.

The humeri are only slightly smaller than in *P. flaviventer* but have a weaker shaft, a wider capital groove, and a reduced bicapital crest. The ulnae hardly differ except in the slightly weaker shafts. The carpometacarpals differ only in slightly smaller size and proportionately shorter intermetacarpal space.

The pelvis is wider in dorsal view and the postacetabular portion is proportionately shorter. Apart from being slightly more robust, it is difficult to detect any differences in the hindlimb elements from those of the living species, particularly given the very limited comparative material available for the latter.

Remarks.—This species differs very little morphologically from *Porzana flaviventer*. Although clearly flightless, the degree of reduction of the wing and pectoral girdle is relatively slight compared with many other flightless rails, probably indicating recency of derivation.

The Yellow-breasted Crake, *P. flaviventer*, is a very small, delicate rail that typically inhabits relatively large bodies of wa-

ter with dense, emergent vegetation. Similar habitats were unlikely to have been present in Bermuda, so the birds must have been able to adapt to different ecological conditions, just as other aquatic rails have adapted to even harsher insular environments on Ascension, St. Helena, and Laysan Islands (Olson 1973b). The modern distribution of *P. flaviventer* includes the Greater Antilles and the Neotropical mainland from southern Mexico to Argentina. An extralimital record from Antigua suggests that the species may have occurred in the Lesser Antilles at least up until about 4300 years ago (Pregill et al. 1988:15).

The Yellow-breasted Crake has never been found historically in Bermuda (Amos 1991). Although it is possible that *P. piercei* was derived from populations of that species in the Greater Antilles, it seems equally plausible that the distribution of *P. flaviventer* may have extended into North America during periods of the Pleistocene, as was shown for the Neotropical rail *Laterallus exilis* (Olson 1974), in which case colonization of Bermuda may have been directly from the North American mainland.

Discussion

Of critical importance is determining the age of the Bermudian avifauna that included at least a crane and a duck with reduced powers of flight and the two species of flightless rails described here. Of these fossils Wetmore (1960:1) could say no more than that "it is certain that they are old, and for the present it is my assumption that they date back to the Pleistocene." Brodkorb (*in* Olson 1977:354) thought that they were "post-Nebraskan, probably Aftonian or Kansan." We now know, however, that the periodicity of sea-level and climatic changes associated with glacial cycles in the Pleistocene was much more complex than the traditional view of the four Nebraskan through Wisconsinan glacial periods, with their intervening interglacials (e.g., Hearty 1998).

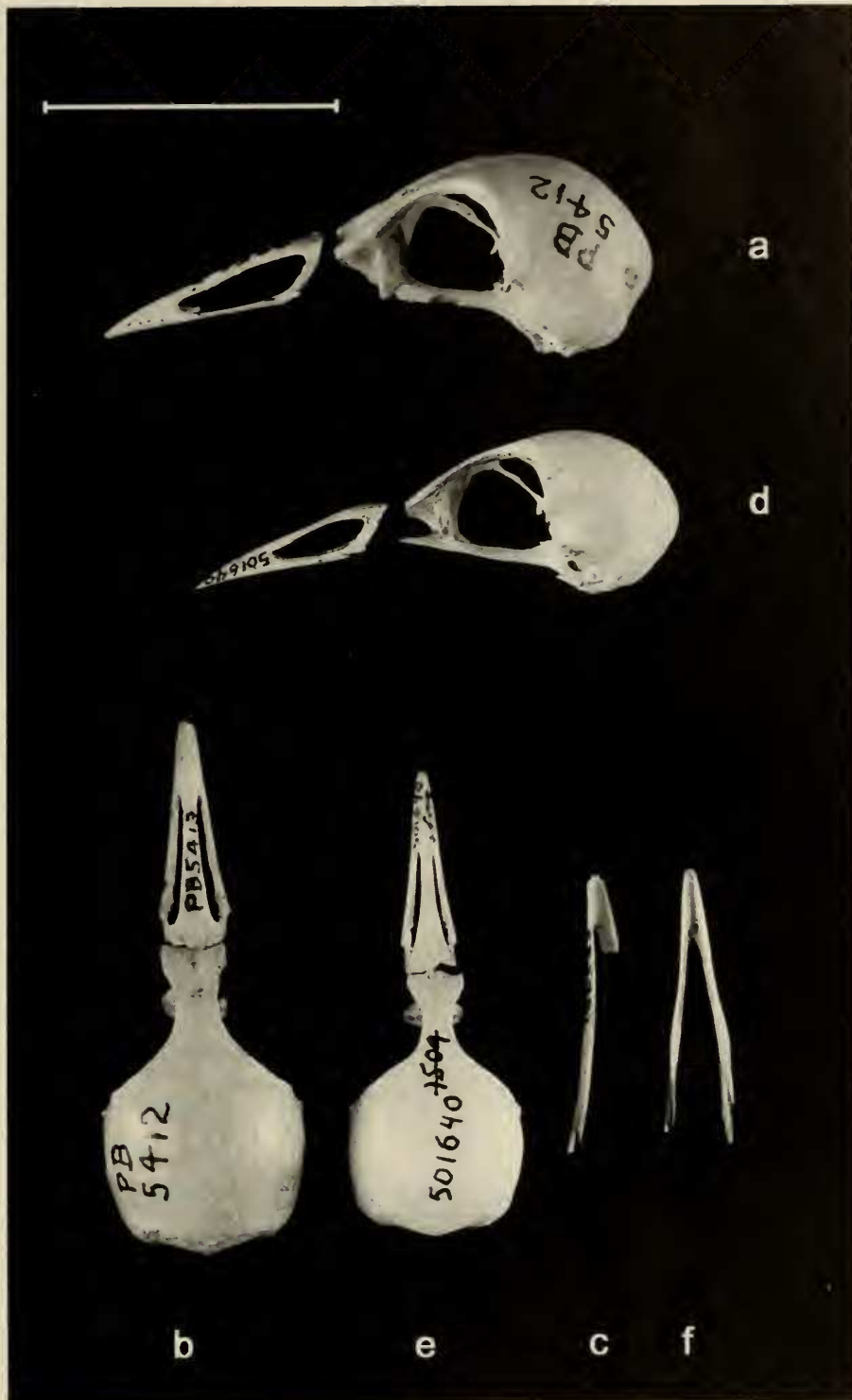


Fig. 6. Comparison of skulls (a–d, lateral view; b–e, dorsal view) and dorsal views of mandibles (c, f) of *Porzana piercei*, new species (a–c) with a very small female *P. flaviventer* USNM 501640 (d–f). a–b, rostrum, holotype UF PB5413, and cranium UF PB5412; c, UF PB5481. Scale bar = 2 cm.

There are as yet no direct radiometric dates on the “crane fauna” of Bermuda but circumstantial evidence points very strongly towards a long period of lowered sea levels in the Middle Pleistocene. The “crane fauna” certainly did not survive into the Holocene as there is no mention of any

such birds in the accounts of early settlers nor are there fossils of these birds in any late Quaternary deposits on the island. To have evolved and sustained such a diverse endemic avifauna, especially including a bird as large as a crane, which would have required extensive savanna-like habitat, the

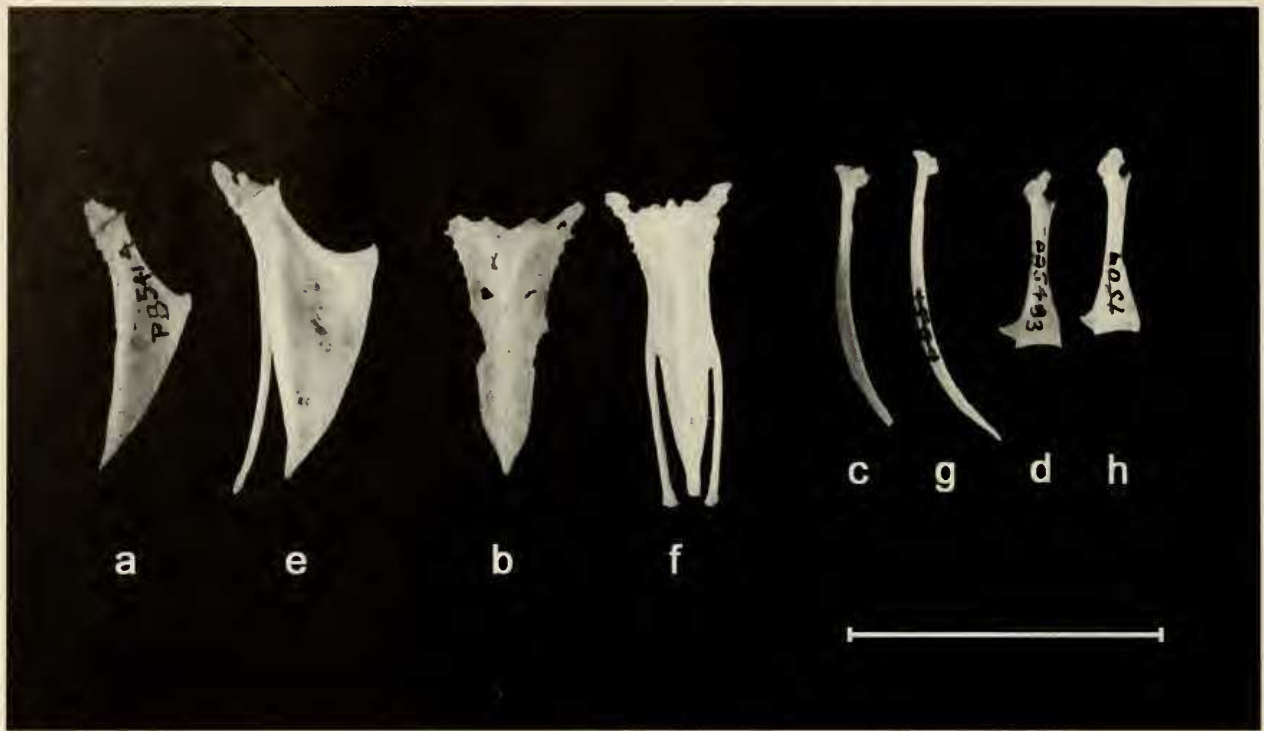


Fig. 7. Comparison of elements of the pectoral girdle of *Porzana piercei*, new species (a–d) with a very small female *P. flaviventer* USNM 501640 (e–h). a–b, sternum UF PB5414 in lateral and ventral views; c, right scapula in dorsal view; UF PB5482; d, left coracoid in ventral view UF PB5483. Scale bar = 2 cm.

land area of Bermuda would have had to be at a maximum for a long period, indicating a glacial period of lowered sea-level of exceptional duration. Thus, Brodkorb's suggestion of Aftonian, which was an interglacial period between the Kansan and Nebraskan glacial epochs, can be ruled out.

Interglacials on Bermuda were periods of marine buildup of carbonate sands on the flooded Bermuda platform, whereas glacial periods were marked by sea-levels well below the surface of the platform when deposition of "terra rossa" soils occurred (Hearty & Vacher 1994). Thus, we would



Fig. 8. Comparison of wing elements of *Porzana piercei*, new species (a–d) with a very small female *P. flaviventer* USNM 501640 (e–g). a–b, left humeri in anconal view UF PB5637 and UF PB5632; c, right ulna in internal view UF PB5485; d, right carpometacarpus UF PB5487. Scale bar = 2 cm.



Fig. 9. Comparison of hindlimb elements in anterior view of *Porzana piercei*, new species (a–f) with *P. flaviventer* (g–i, USNM 501640 small female; j–l, USNM 561276 unsexed). a, right femur UF PB5478; b, right femur UF PB5488; c, right tibiotarsus UF PB5470; d, right tibiotarsus UF PB5510; e, right tarsometatarsus UF PB9229; f, right tarsometatarsus UF PB5590. Scale bar = 2 cm.

expect deposition of fossils associated with “terra rossa” soils in caves and fissure fills to have taken place mainly during periods of lowered sea levels. The longest and most stable period of lowered sea-levels in the Quaternary history of Bermuda was from Oxygen Isotope Stage 13 back to about Stage 21 (Hearty & Vacher 1994:687, table 1), which spanned a period from about 450 kya to about 800 kya. Although sea-levels fluctuated during this time, as shown by the various isotope stages, the amplitude of the fluctuations was greatly reduced. Thus, even during the highest stands, the sea was at or below the level of the Bermuda platform through the preponderance of this interval, during which the subaerial portion of the platform would have been at its maximum extent. It was during this time that deep limestone dissolution (karstification) and the accumulation of a massive “terra rossa” soil, the Castle Harbour Geosol, occurred (Hearty & Vacher 1994).

This span of several hundred thousand years of maximum island emergence and relatively stable terrestrial conditions would probably have been the only time during Bermuda’s Pleistocene history when the

“crane fauna” could have developed. Subsequent events also provide a very convincing explanation for the disappearance of this fauna, for it is now known that during interglacial Stage 11, 380 to 440 kya, sea levels rose much higher than had previously been documented (Hearty et al. 1999), reaching a height of over 20 m above present level. This would have reduced the land area of Bermuda by two orders of magnitude, so that only a few small islets would have remained. In terms of the terrestrial biota, this event would essentially have wiped the slate clean, eliminating the crane, duck, and rails. A new period of colonization and adaptation during the next glacial period probably resulted in a substantially different avifauna.

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